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Influence of plant size and species on preference of *Cyrtobagous salviniae* adults from two populations

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Abstract

Adults from two populations (Brazil and Florida) of *Cyrtobagous salviniae* were bioassayed to determine if they exhibited a preference for either *Salvinia minima* or *Salvinia molesta*. Adults did not discriminate between host species in initial tests that evaluated the tertiary growth form. Further tests which compared two growth forms (primary and tertiary) as well as plant species, found that adults from the Brazil population consistently preferred larger (tertiary) plants without regard for host species. Weevils from the Florida population showed a similar, but less distinct, pattern of preference. Although adults from the Florida population survived equally well and experienced a similar pre-oviposition period on both plant species, they laid more eggs in *S. molesta*. Adults from the two populations differ in size: Brazil weevils were larger, which may explain their sensitivity to plant size as compared with the smaller Florida adults. Narrower rhizomes in *S. minima* may restrict usage of this species by the larger weevils, whereas smaller larvae may be better able to burrow in a wider range of plant sizes. Both weevil populations should be suitable biological control agents for use in programs targeting *S. molesta*.
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Keywords: *Cyrtobagous salviniae*; *Salvinia molesta*; *Salvinia minima*; Host preference; Biological control

1. Introduction

Giant salvinia, *Salvinia molesta* D.S. Mitchell, and common salvinia, *Salvinia minima* Baker (*Salviniaceae*), are problematic aquatic weeds of South American origin now established in the United States. Although *S. molesta* is considered the greater problem, *S. minima* is degrading wetland ecosystems in several states in the US (Julien et al., 2002). Both species of these free-floating ferns quickly cover and dominate stagnant and slow-flowing fresh water systems. Giant salvinia has spread around the world and caused problems in regions of Africa, Australia, and Asia, and has recently established in North America (Jacono, 1999). The earliest detection in 1995 in South Carolina was purportedly eradicated before it could spread. However, in 1998, multiple infestations appeared in several eastern Texas drainages. These were of such size, complexity, and number that eradication was not feasible. Management programs utilizing herbicides and biological control are now underway. Similar efforts are directed at common salvinia in Louisiana where the plant is much more aggressive than in Florida. This differential aggressiveness of this plant in these states may be related to the effects of *Cyrtobagous salviniae* Calder and Sands (Coleoptera: Curculionidae) which is present in Florida but not Louisiana (Jacono et al., 2001).

Cyrtobagous salviniae has successfully controlled giant salvinia, *S. molesta*, in 13 countries over three continents (Julien and Griffiths, 1998). The weevil found feeding on *S. molesta* in south-eastern Brazil during 1978 (Forno and Harley, 1979) was presumed to be *Cyrtobagous singularis* Hustache, which had earlier been collected from *Salvinia auriculata* in Trinidad and Guyana

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and released in Africa and Fiji with little effect on *S. molesta* (Bennett, 1966). This Brazilian weevil was released, after extensive host-specificity testing, on Lake Moondarra in Queensland where the weed infestation was reduced 99% in under 12 months (Room et al., 1981). Careful examination of this weevil revealed subtle morphological differences, when compared to the Trinidad specimen, that were sufficient to elevate it to species status. It was subsequently described as *C. salviniae* (Calder and Sands, 1985). Weevils from Florida (Florida population), collected from *S. minima*, were also identified as *C. salviniae* despite an earlier misidentification as *C. singularis* (Kissinger, 1966). Calder and Sands (1985) also noted that *C. salviniae* from *S. minima* in Florida were significantly smaller than the *C. salviniae* collected on *S. molesta* from Brazil (Brazil population).

A biological control project targeting *S. molesta* was initiated in Texas and Louisiana in 1999 utilizing *C. salviniae* collected from *S. minima* in Florida. This approach minimized the risk of introducing natural enemies with *C. salvinia* populations from other parts of the world. The geographic range and distribution of *S. minima* and *C. salviniae* in the US was examined by Jacono et al. (2001) who found that the weevil occurs throughout Florida while *S. minima* is present in Florida, Louisiana, Texas, and five other states. The first releases of the Florida population were not successful presumably because of deterioration of weevil fitness during shipment and then destruction of release sites by herbicide applications, drought, or floods. This prompted various authorities to question whether the Florida population was suitable, suggesting that it is specialized on *S. minima* and was maladapted to *S. molesta*.

This view was supported by a comparison of the D2 expansion domain of the 28S rRNA gene between the Florida and Brazil population of *C. salviniae*, which yielded consistent variation at 10 polymorphic positions (Goolsby et al., 2000). The biological significance of these data were unclear inasmuch as the comparison did not include an outgroup like *C. singularis*, but they raised questions about the identity of the Florida population. This led to a temporary cessation of further releases and refocused efforts on release of the Brazil population of *C. salviniae* that was acquired from Australia. However, recent molecular studies, using *C. singularis* as an outgroup, indicate that the two populations are genetically very similar (P. Madeira, USDA-ARS, Invasive Plant Research Laboratory, Ft. Lauderdale, Florida, personal communication).

Our objective was to evaluate both weevil populations to determine whether either exhibited a preference for *S. molesta* or *S. minima*. In this study, we define preference as a behavioral response of the adults to the plants as suggested by Singer (2000). Hereafter, we refer to the two weevil populations as “Florida” or “Brazil” *C. salviniae*.

2. Materials and methods

2.1. Preference of Florida adults for the tertiary growth form of S. minima or S. molesta

Both salvinia species exhibit three basic growth forms, depending upon the degree of crowding of the plant: primary, secondary, and tertiary (Mitchell and Tur, 1975). The primary growth form is usually present in low-density populations and is characterized by smaller plants with leaves that lie flat on the water surface. In comparison, plants in the tertiary form are found under dense growing conditions with larger leaves folded vertically so that most of their surface is off the water surface. Only the tertiary growth form was used in this first experiment. The secondary growth form is intermediate and was not used in any of the testing.

Treatments were combinations of two plants in the tertiary growth form of *S. molesta* and *S. minima* placed in a film of tap water in the center of a plastic container (15.3×3.8 cm). A line was drawn through the center of each dish, thereby dividing the arena into two equal areas designated as position one and two. Treatment combinations were: (1) two plants of *S. molesta*, (2) two plants of *S. minima*, and (3) one plant each of *S. molesta* and *S. minima*. Plant biomass was equalized for each position.

Plants were randomly assigned to a position (one or two). A plant was defined as a group of 3–4 ramets attached by a common rhizome. All plants were obtained from laboratory colonies and were gently washed in tap water to remove detritus, blotted dry with a paper towel, and arranged so as many leaves as possible from both plants were in direct contact. Ten adults (6 ♀: 4 ♂) of Florida *C. salviniae*, field-collected from *S. minima*, were released in a central area at the interface of both plants. Containers were closed and held in an environmental chamber at 27.7 °C and 12:12 h (L:D) photophase. The plants were examined every 24 h by gently lifting the leaves to locate adults without disturbing them. The number of adults found in three locations (leaf, rhizome, ‘root’) were recorded. Adults found off the plants, floating in the water, or on the sides of the container were not counted but set aside to be placed back in their original release location after the remaining adults on the plants were counted. The plants were replaced as closely as possible to their original positions and the containers were returned to the environmental chamber. Fifteen replications were performed and the tests were ended after 72 h.

2.2. Preference of Florida and Brazil adults for two growth forms of S. minima and S. molesta

The experimental design was a $2 \times 2 \times 2$ factorial in a randomized complete block with two *Salvinia* species, two *C. salviniae* populations, and two plant forms (1° and 3°). There were 15 and 12 replications for the Brazil and Florida populations, respectively. Leaf lengths were measured to the nearest 0.1 cm along the long axis of the pair of leaves located at the second internode proximal to the terminal bud of the rhizome. Rhizome width for 40 plants was also recorded to the nearest 0.1 mm at the same location. Treatments were all pairwise combinations of two species and growth forms ($n = 10$) placed in the center of the arena in a film of tap water as before. Unlike the previous test, only five *C. salviniae* adults (3♀: 2♂), were released in the central area at the interface between both plants as before and held in an environmental chamber at 27.7 °C and 12:12 h (L:D) photophase. Fewer adults were used in this experiment to avoid crowding effects. These adults were from laboratory colonies with the Brazil population raised on *S. molesta* and the Florida population raised on *S. minima*.

2.3. Longevity, pre-oviposition period, and fecundity of florida *C. salviniae* on *S. minima* and *S. molesta*

To obtain adults of similar ages, *S. minima* in selected tanks were regularly submerged in situ for 24 h. A few *S. minima* plants floating on the water's surface served as traps for surfacing adults which were then easily collected. These were then separated by color. Adults that had recently emerged from pupae were recognized by their light brown color. They were set aside for the experiment while older, dark brown adults were returned to the tanks. Groups of weevils were placed on *S. minima* or *S. molesta* and permitted to feed for 15 days to mate and maturate eggs. Adults were then removed, separated by gender, and placed on a single plant (3–4 ramets, tertiary growth form) of *S. minima* or *S. molesta* in 35-ml plastic cups. Plants were replaced every 3–5 days. Dead males were recorded and replaced from the original stock of light brown adults. Testing with a specific mating pair was terminated when the female died. Plants were floated in a nutrient solution containing 5 ppm soluble nitrogen and placed in an environmental chamber set at 25 °C with a 12 h photoperiod.

After the weevils were transferred to new plants, the entire original plant was dissected and numbers of eggs were recorded. All eggs were removed and placed on moistened filter paper in a standard, 15-cm plastic petri dish until they hatched.

2.4. Average weights of Brazil and Florida *C. salviniae*

Over a 19-month period, adults from both populations were collected from laboratory colonies and weighed. A total of 219 and 184 adults were sampled from the Brazil and Florida populations, respectively. Adults were placed in standard 15 cm petri dishes for 1 h to air dry, then weighed individually to the nearest 0.1 mg.

Table 1
Means (±SE) of the total number of *C. salviniae* adults from the Florida population found on tertiary growth form plants of *S. minima* or *S. molesta* after 72 h in laboratory tests

Treatment number	Salvinia species	Mean no. *C. salviniae* adults		t	P
	Position #1/ Position #2	Position #1	Position #2		
1	*S. minima*/ *S. minima*	4.0 ± 0.6	4.6 ± 0.1	−0.97	0.358
2	*S. minima*/ *S. molesta*	4.3 ± 0.4	4.8 ± 0.4	0.79	0.453
3	*S. molesta*/ *S. molesta*	4.5 ± 0.3	5.1 ± 0.3	−1.39	0.202

2.5. Analysis

Adult preference was determined using two-sample t tests to compare the mean total number of adults between positions found at each sample period. Frequencies were further analyzed using Fisher's Exact Test (SAS, 1990) to examine the relationship between adult weevils' response and plant variables (i.e., species and size). This approach was used because the counts in each cell in the cross-tabulation tables were usually less than five. Adult longevity, the length of the pre-oviposition period, and fecundity data were analyzed using ANOVA (SAS, 1990). Adult mean weights between populations were compared using a two-sample t test. The relationship between leaf length and rhizome width was examined using regression analyses. Chi-square tests were used to determine whether the intra-plant dispersion of adults was independent of plant species.

3. Results and discussion

In the first test, using tertiary growth-stage plants, adults of Florida *C. salviniae* showed no preference for either *Salvinia* species ($t = 0.79$; $df = 28$; $P = 0.453$) (Table 1, treatment 2). These data suggest that the original idea of releasing Florida *C. salviniae* against *S. molesta* in Texas was sound. Additional confirmation of this approach was provided in 2001 when a recently discovered infestation of *S. molesta* near Naples, Florida was found to be heavily attacked by the Florida population (Tipping, personal observation). One reason for limiting imports of beneficial agents is to reduce the risk of introducing their natural enemies or diseases. In fact, a shipment of *C. salviniae* from South Africa (Brazil population) was found in quarantine to be infected with a unknown *Helicosporidium* sp. and was subsequently destroyed (Genie White, USDA-ARS-CMAVE, Gainesville, Florida, personal communication).

The second preference experiment with both weevil populations again indicated that plant species was not an

Table 2
Means (±SE) number of *C. salviniae* adults from the Brazil population found on primary or tertiary growth form plants of *S. minima* and *S. molesta* after 72 h of exposure in laboratory tests

Treatment number	Species-growth stage	Mean no. *C. salviniae* adults[a]		t	P
	Position #1/Position #2	Position #1	Position #2		
1	*S. minima*-1°/*S. minima*-1°	2.0 ± 0.1 ns	1.8 ± 0.1	1.19	0.26
2	*S. minima*-1°/*S. minima*-3°	1.3 ± 0.2	3.0 ± 0.1[a]	−6.05	<0.01
3	*S. minima*-3°/*S. minima*-3°	2.4 ± 0.3 ns	2.2 ± 0.3	0.46	0.65
4	*S. minima*-1°/*S. molesta*-1°	1.9 ± 0.2 ns	2.7 ± 0.2	−2.06	0.07
5	*S. minima*-1°/*S. molesta*-3°	1.5 ± 0.3	3.2 ± 0.2[a]	−3.76	<0.01
6	*S. minima*-3°/*S. molesta*-1°	2.6 ± 0.1[a]	1.8 ± 0.2	2.98	0.01
7	*S. minima*-3°/*S. molesta*-3°	1.8 ± 0.2	2.8 ± 0.2[a]	−2.54	0.03
8	*S. molesta*-1°/*S. molesta*-1°	2.4 ± 0.1 ns	1.9 ± 3.3	1.08	0.31
9	*S. molesta*-1°/*S. molesta*-3°	1.2 ± 0.1	3.6 ± 0.1[a]	−11.50	<0.01
10	*S. molesta*-3°/*S. molesta*-3°	2.4 ± 0.1 ns	2.2 ± 0.1	1.14	0.28

[a] Indicates that the plant in that position was larger than the one in the opposite position ($P = 0.05$). Ns, indicates plants were of equal size.

Table 3
Means (±SE) number of *C. salviniae* adults from the Florida population found on primary or tertiary growth form plants of *S. minima* and *S. molesta* after 72 h of exposure in laboratory tests

Treatment number	Species-growth stage	Mean no. *C. salviniae* adults[a]		t	P
	Position #1/Position #2	Position #1	Position #2		
1	*S. minima*-1°/*S. minima*-1°	2.1 ± 0.2 ns	2.5 ± 0.1	−1.35	0.23
2	*S. minima*-1°/*S. minima*-3°	0.8 ± 0.1	2.4 ± 0.8[a]	−1.95	0.09
3	*S. minima*-3°/*S. minima*-3°	2.0 ± 0.3 ns	1.4 ± 0.4	1.13	0.29
4	*S. minima*-1°/*S. molesta*-1°	1.3 ± 0.4 ns	3.0 ± 0.6	−2.12	0.07
5	*S. minima*-1°/*S. molesta*-3°	1.3 ± 0.6	2.8 ± 0.4[a]	−1.96	0.09
6	*S. minima*-3°/*S. molesta*-1°	2.7 ± 0.6[a]	1.6 ± 0.2	1.59	0.18
7	*S. minima*-3°/*S. molesta*-3°	1.6 ± 0.4	2.7 ± 0.2[a]	−2.09	0.08
8	*S. molesta*-1°/*S. molesta*-1°	1.7 ± 0.1 ns	2.5 ± 0.4	−1.50	0.18
9	*S. molesta*-1°/*S. molesta*-3°	1.3 ± 0.1	3.0 ± 0.3[a]	−4.52	<0.01
10	*S. molesta*-3°/*S. molesta*-3°	2.1 ± 0.3 ns	2.5 ± 0.3	−0.68	0.52

[a] Indicates that the plant in that position was larger than the one in the opposite position ($P = 0.05$). Ns, indicates plants were of equal size.

Table 4
Means (±SE) of the leaf lengths from primary and tertiary growth form plants of *S. minima* and *S. molesta* used in comparison tests

Species-growth form		Mean leaf length (cm)		t	P
Position #1	Position #2	Position #1	Position #2		
S. minima-1°	*S. minima*-1°	0.74 ± 0.03	0.81 ± 0.03	−1.30	0.24
S. minima-1°	*S. minima*-3°	0.76 ± 0.02	1.17 ± 0.04	−4.12	<0.01
S. minima-3°	*S. minima*-3°	1.11 ± 0.12	1.08 ± 0.10	0.18	0.86
S. minima-1°	*S. molesta*-1°	0.79 ± 0.01	0.78 ± 0.01	0.15	0.88
S. minima-1°	*S. molesta*-3°	0.79 ± 0.04	1.38 ± 0.15	−3.71	<0.01
S. minima-3°	*S. molesta*-1°	1.09 ± 0.08	0.84 ± 0.01	2.92	0.02
S. minima-3°	*S. molesta*-3°	1.07 ± 0.12	1.54 ± 0.06	−3.40	0.01
S. molesta-1°	*S. molesta*-1°	0.82 ± 0.05	0.78 ± 0.03	0.68	0.52
S. molesta-1°	*S. molesta*-3°	0.89 ± 0.02	1.49 ± 0.05	−9.88	<0.01
S. molesta-3°	*S. molesta*-3°	1.47 ± 0.03	1.47 ± 0.04	−0.07	0.94

important determinant in adult preference. Instead, adult preference was based on plant size, although this was less evident in the Florida population (Tables 2 and 3). Adults from the Brazil population selected the larger plant, regardless of species, in all comparisons that resulted in significant adult preferences (Table 2). The average leaf lengths of primary and tertiary *S. minima* and *S. molesta* used in the experiment are listed in Table 4. Although the pattern of preference in the Florida population was similar, there was only one significant comparison at $P = 0.05$ (Table 3). In that case, the adults chose the larger plant over the smaller one (treatment 9, Table 3). However, the same pattern of preferences, i.e., larger plants over smaller plants regardless of species, was evident in the tests with the Florida population when the α level was raised to 0.1. Although there is an increased risk of a Type I error by raising α, doing so reveals a consistent trend that mirrors the preference of the Brazil population for plant size rather than for plant species.

We found a significant positive relationship between plant size and adult preference using the same α level and by constructing a cross-tabulation table using adult pref-

Table 5
Cross-tabulation table with frequency distribution of adult *C. salviniae* preference response to plant size and species

Weevil population		Frequency of tests (%) and adult response		
		Adult preference exhibited		
		Yes	No	
Brazil	Same plant size	1 (10)	4 (40)	$P = 0.04$[a]
	Different plant size	5 (50)	0 (0)	
Florida	Same plant size	1 (10)	5 (50)	$P = 0.04$
	Different plant size	4 (40)	0 (0)	
Brazil	Same plant species	2 (20)	4 (40)	$P = 0.07$
	Different plant species	4 (40)	0 (0)	
Florida	Same growth stage	2 (20)	4 (40)	$P = 0.52$
	Different growth stage	3 (30)	1 (10)	

[a] Fisher's Exact Test (SAS, 1990).

erence and plant parameters (species and size) (Table 5). When plant species were grouped with adult preference, there was no relationship with the Florida population but there did appear to be one with the Brazil adults. However, closer examination found that plants of different sizes were involved in three of the four comparisons where adults seemed to exhibit a host preference (Table 3; treatments 5, 6, and 7), indicating that size is a major determinant in preference. For example, adults in treatment 5 preferred the larger growth form of *S. minima* to the smaller growth form of *S. molesta*. The reciprocal treatment (# 6) again showed that adults preferred the larger plant, although in this case the preferred species was *S. molesta*.

This population difference in adult preference may be explained by a different sensitivity to plant size. The Brazil population has larger individuals than the Florida population which may motivate the adults to seek plants with rhizomes of a sufficient diameter for the burrowing activity of immatures ($t = 8.95$, $df = 401$, $P < 0.001$) (Fig. 1). Leaf length positively correlated with rhizome width ($r^2 = 0.91$, $n = 40$) (Fig. 2). Florida adults and larvae are smaller, which may allow them to utilize smaller plants, perhaps resulting in less discrimination on the basis of size as long as some minimum plant size is available.

The consistency of insect numbers on each plant at each sample period suggests that once a plant was chosen there was no wholesale movement from one plant to another (data not shown). Although individual adults were not marked, this species is not very active, making it unlikely that any significant movement of adults occurred after their initial choice was made within 24 h.

The locations on the plants where *C. salviniae* were found during testing were not independent of *Salvinia* species. These interactions, while significant, are difficult to interpret. For example, in the first experiment using tertiary growth forms only, adults from the Florida population were found less frequently than expected on *S. minima* leaves and rhizomes and more frequently than

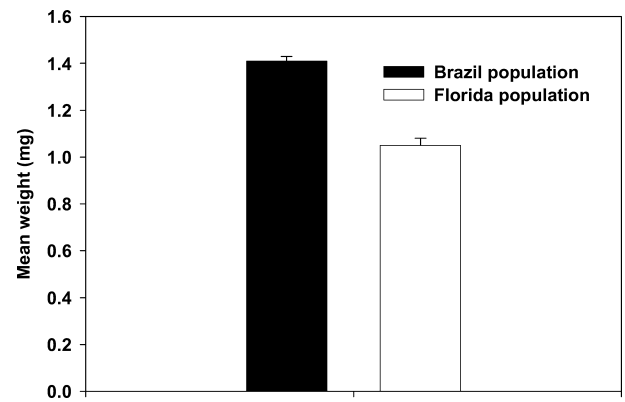

Fig. 1. Mean weights of adult *C. salviniae* from Brazil and Florida populations.

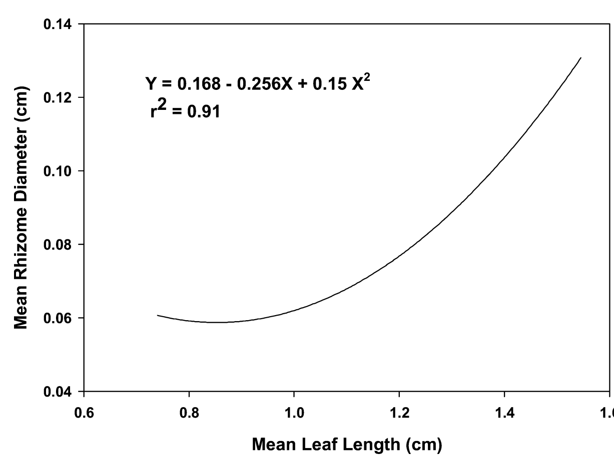

Fig. 2. Relationship between mean leaf length and rhizome width for *S. minima* and *S. molesta.*

expected on 'roots.' (These species lack true roots but rather bear highly dissected submerged leaves that resemble roots). At the same time, adults were detected more frequently than expected on the leaves and rhizomes of *S. molesta* and less than expected on 'roots' ($\chi^2 = 9.16$, $P = 0.01$). This pattern was not consistent in the next round of experiments where adults of both

Table 6
Means (±SE) of the longevity, length of pre-oviposition period, and number of eggs oviposited by Florida *C. salviniae* females reared on *S. minima* or *S. molesta* in laboratory tests

Variable	*n*	*S. minima*	*n*	*S. molesta*	*t*	*P*
Longevity (days)	13	96.1 ± 12.9	10	104.9 ± 18.5	−0.39	0.70
Pre-oviposition period (days)	3	44.6 ± 9.0	5	43.0 ± 3.3	0.17	0.87
No. eggs per ♀	8	1.0 ± 0.6	6	23.1 ± 10.2	−2.53	0.02

weevil populations were found more often than expected on *S. minima* leaves but less than expected on rhizomes and 'roots.' The results on *S. molesta* were exactly the opposite: fewer weevils on leaves, more on rhizomes and 'roots' ($\chi^2 = 21.36$, $P < 0.001$ and $\chi^2 = 22.57$, $P < 0.001$ for Florida and Brazil populations, respectively).

There were no differences in adult longevity and the length of the pre-oviposition period for Florida *C. salvinia* adults raised on *S. minima* or *S. molesta*. However, more eggs were produced per female by adults feeding on *S. molesta* (Table 6). Although larger scale studies are needed here, it is instructive that the Florida population successfully oviposited in *S. molesta*, thereby confirming the appropriateness of their deployment against this weed. Despite the fact that eggs are extremely fragile and easily damaged during removal from plant tissue, more than 75% of all eggs collected hatched.

These data indicate that the populations of *C. salviniae* adults showed no preference between *Salvinia* species, but rather selected host plants on the basis of growth form, which was directly related to plant size. There is precedence for adult preference based on plant size for boring and galling insects (Craig et al., 1989; Smith and Story, 2003). Although adult preference does not always translate into offspring performance, there are examples where larger gall sizes or stem diameters increase larval survival by reducing factors like parasitism (Abrahamson et al., 1989) or intraspecific competition (Mook and Van der Toorn, 1985). It has yet to be determined if larger rhizomes promote offspring performance in salvinia but there is evidence that feeding within the rhizomes increases both larval survivability and overall damage to the plant (Sands et al., 1986; Sands and Schotz, 1985). We conclude that either population of *C. salviniae* would be suitable for use in biological control programs targeting *S. molesta*.

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